The dimensionality of stability depends on disturbance type

Radchuk, Viktoriia; DE LAENDER, Frederik; Cabral, Juliano Sarmento; Boulangeat, Isabelle; Crawford, Michael; Bohn, Friedrich; Raedt, Jonathan De; Scherer, Cédric; Svenning, Jens Christian; Thonicke, Kirsten; Schurr, Frank M.; Grimm, Volker; Kramer-Schadt, Stephanie

Published in:
Ecology Letters

DOI:
10.1111/ele.13226

Publication date:
2019

Document Version
Peer reviewed version

The dimensionality of stability depends on disturbance type

Running title: dimensionality of ecological stability

Viktoriia Radchuk[1], Frederik De Laender[2], Juliano Sarmento Cabral[3], Isabelle Boulangeat[4,5], Michael Crawford[6], Friedrich Bohn[7], Jonathan De Raedt[2,8], Cédric Scherer[1], Jens-Christian Svenning[4,9], Kirsten Thonicke[10], Frank Schurr[11], Volker Grimm[7,6,12], Stephanie Kramer-Schadt[1,13]

[1] Department of Ecological Dynamics, Leibniz Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17, Berlin, Germany, radchuk@izw-berlin.de, scherer@izw-berlin.de

[2] Institute of Life-Earth-Environment, Namur Institute of Complex Systems, Research Unit in Environmental and Evolutionary Biology. Université de Namur, Rue de Bruxelles 61, Namur, Belgium, frederik.delaender@unamur.be

[3] Ecosystem Modeling, Center for Computational and Theoretical Biology (CCTB), University of Würzburg, Campus Hubland Nord, Würzburg, Germany, juliano.sarmento_cabral@uni-wuerzburg.de

[4] Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 116, Aarhus, Denmark, isabelle.boulangeat@gmail.com

[5] Univ. Grenoble Alpes, Irstea, UR LESSEM, 2 rue de la Papeterie-BP 76, F-38402 St-Martin-d'Hères, France

[6] Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, Potsdam, Germany, mscrawfor@gmail.com

[7] Department of Ecological Modelling, Helmholtz Centre for Environmental Research – UFZ, Permoserstr. 15, Leipzig, Germany, friedrich.bohn@ufz.de

[8] Laboratory of Environmental Toxicology and Aquatic Ecology, Ghent University, Coupure Links 653, Ghent, Belgium, jonathan.deraedt@ugent.be

[9] Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Ny Munkegade 114, Aarhus, Denmark, svenning@bios.au.dk

[10] Research Domain 1 "Earth System Analysis", Potsdam Institute for Climate Impact Research (PIK), Telegrafenberg A31, Potsdam, Germany, kirsten.thonicke@pik-potsdam.de

[11] Institute of Landscape and Plant Ecology, University of Hohenheim, August-von-Hartmann-Str. 3, Stuttgart, Germany, frank.schurr@uni-hohenheim.de

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Français (Belgique)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

[12] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig, Germany, volker.grimm@ufz.de

[13] Department of Ecology, Technische Universität Berlin, Rothenburgstrasse 12, 12165 Berlin, kramer@izw-berlin.de

Corresponding author: radchuk@izw-berlin.de

This manuscript type is a Letter

Word count in abstract: 150

Word count main text: 4951

Word count in Glossary: 310

Number of references: 55

Number of figures: 5

Number of tables: 0

Statement of authorship: All authors discussed and agreed on the experimental design; MC, FB, JDR, CS and VR run the simulations; VR performed the analyses of stability; VR wrote the first draft of the manuscript and all authors contributed substantially to revisions.

Data accessibility statement: should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad or Figshare) and the data DOI will be included at the end of the article.

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Code de champ modifié
Mis en forme : Anglais (États-Unis)

ABSTRACT

Ecosystems respond in various ways to disturbances. Quantifying ecological stability therefore requires inspecting multiple stability properties, such as resistance, recovery, persistence, and invariability. Correlations among these properties can reduce the dimensionality of stability, simplifying the study of environmental effects on ecosystems. A key question is how the kind of disturbance affects these correlations. We here investigated the effect of three disturbance types (random, species-specific, local) applied at four intensity levels, on the dimensionality of stability at the population and community level. We used previously parameterized models that represent five natural communities, varying in species richness and the number of trophic levels. We found that disturbance type but not intensity affected the dimensionality of stability and only at the population level. The dimensionality of stability also varied greatly among species and communities. Therefore, studying stability cannot be simplified to using a single metric and multi-dimensional assessments are still to be recommended.

Keywords: Community model, persistence, resistance, invariability, recovery, extinction, disturbance intensity, disturbance type, individual-based model

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

GLOSSARY

State variables are variables used to quantify stability properties of a system, i.e. a population or a community in the context of this study. Examples of state variables are abundance (population level) and species richness or total abundance (community level).

Resistance is the degree to which a state variable is changed following a disturbance (Pimm 1984), here measured as the difference between a perturbed and a control system at the first sampling after the treatment (Hillebrand *et al.* 2018).

Recovery is the capacity of a system to return to its undisturbed state following a disturbance (Ingrisch & Bahn 2018), here measured as the degree of change in a state variable of a perturbed compared to a control system at the last sampling (Hillebrand *et al.* 2018).

Persistence is the existence of a system through time as an identifiable unit (Pimm 1984; Grimm & Wissel 1997), measured by the time during which a system maintains the same state (i.e., state variables within certain ranges) before it changes in some defined way (Donohue *et al.* 2016).

Invariability reflects the temporal constancy of a state variable following the disturbance, usually measured as the inverse of temporal variability of a state variable (Wang *et al.* 2017). Higher invariability indicates higher stability (Donohue *et al.* 2013).

Disturbance is a change in the biotic or abiotic environment that alters the structure and dynamics of a system (Donohue et al. 2016).

Stability is a multidimensional concept that tries to capture the different aspects of the dynamics of the system and its response to perturbations (Donohue *et al.* 2016). Here, we consider the following stability properties: resistance, recovery, persistence, and variability.

Mis en forme : Anglais (États-Unis)

The **dimensionality of stability** (DS) depends on the strength of correlations among stability properties. Low correlation corresponds to high dimensionality. If dimensionality is high, a single stability measure cannot be used as a sole indicator of the overall system stability (Donohue *et al.* 2013).

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

INTRODUCTION

Understanding the response of populations, communities, and ecosystems to fast, human-induced environmental changes is a key challenge (Carpenter *et al.* 2011; Higgins & Scheiter 2012; Scheffer *et al.* 2015; DeLaender *et al.* 2016). However, quantifying the stability of natural systems is challenging because stability is a multidimensional concept and requires measuring several stability properties such as *resistance*, *recovery*, *persistence*, and *invariability* (see Glossary, Pimm 1984; Grimm & Wissel 1997; Donohue *et al.* 2016). Correlation among these properties manifests the dimensionality of stability (DS): if the stability properties strongly correlate, the dimensionality is low, and *vice versa* (Donohue *et al.* 2013; Hillebrand *et al.* 2018, Fig. 1a,b). Theory underpinning DS is still in its infancy (Donohue *et al.* 2013) and relevant empirical evidence is only beginning to accumulate (Donohue *et al.* 2013; Hillebrand *et al.* 2018). A key question is whether DS depends on the kind of underlying disturbance. Donohue *et al.* (2013) showed that when disturbed by consumer removal, DS increased in marine shore communities. At present it is unclear if such conclusions can be extrapolated to other kinds of disturbance.

There are many kinds of disturbance. Disturbance properties include: duration, spatial extent, intensity, frequency, and type (Turner 2010). According to their *duration*, two extreme classes of disturbance can be distinguished: pulse disturbances (e.g. fire or flooding) occur over a short time scale, relative to the typical speed at which a system changes, and press disturbances (e.g. global warming or exploitation) represent a constant, long-term change. Disturbance *intensity* reflects how much individuals / biomass are affected by an event over a period of time (Turner 2010). Disturbance *frequency* reflects how often disturbance events occur within a given

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Commenté [FDL1]: There's a space missing: 'De Laender', not 'DeLaender'

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

time period. Examples of disturbance *types* are local vs. global, and selective vs. non-selective disturbances (De Laender *et al.* 2016).

Despite increasing understanding of how disturbances affect each single stability property, we know little of how the kind of disturbance affects the relationships among multiple stability properties, i.e. the dimensionality of stability (Donohue *et al.* 2013). Yet, such knowledge is crucial for guiding efforts to monitor and manage natural systems. Indeed, if several stability properties correlate strongly irrespective of the properties of disturbances acting on them, the stability of the overall system reduces to one dimension (i.e. low DS, Fig. 1a). This means that monitoring schemes could be optimized by quantifying only a few stability properties. ~~Vice versa~~Alternatively, if a system's stability properties are poorly correlated (i.e. high dimensionality), inferring the system's overall stability requires measuring all ~~of them~~properties (Fig. 1b). Therefore, management of natural systems would profit from knowing how DS is influenced by different disturbance properties. For example, an increase of dimensionality with disturbance intensity would undermine the main assumption for detecting tipping points (Dakos *et al.* 2012; Dai *et al.* 2015) through early warning signals (e.g. coefficient of variation, temporal autocorrelation), which usually manifest the variability of a system.

DS can be decomposed into pair-wise correlations among underlying stability properties (Donohue *et al.* 2013; Hillebrand *et al.* 2018; Pennekamp *et al.* 2018). We generally expect positive pair-wise correlations between invariability, resistance, recovery and persistence. For example, ~~at the population level~~ invariability and persistence are expected to correlate positively at the population level, because the higher the temporal constancy in population size, the more likely the population is to persist (Ginzburg *et al.* 1982; Inchausti & Halley 2003). Similarly, at the community level, the higher the temporal constancy in community composition, the more

Mis en forme : Anglais (États-Unis)

likely this community is to persist in its unchanged state. For arguments of why we expect other stability properties to correlate positively, see Table S1 in Supporting Information. Because pair-wise correlations are 'constituents' of DS, they are expected to depend on the same factors as DS: disturbance properties and the level of organization. Indeed, the sign of a pair-wise correlation between stability properties was shown to change when, instead of a single disturbance, two disturbance types were applied simultaneously to yeast populations (Dai *et al.* 2015). Also, pair-wise correlations measured at the community and ecosystem level differed in plankton communities disturbed by reduced light availability (Hillebrand *et al.* 2018). Understanding whether pair-wise correlations are affected similarly ~~by~~ across ~~disturbances irrespective of~~different disturbance types and study systems would facilitate more efficient monitoring of the stability of natural systems.

Here, we used process-based, spatially-explicit models to assess how the intensity and the type of disturbance affect DS at the population and community levels. Our models are well tested and structurally realistic, and represent five different communities: a species-rich temperate grassland community, a temperate forest, an algae community, a boreal predator-prey system, and a host-pathogen system. The modelled communities varied in species richness (2 up to 86 species) and number of trophic levels (one or two). At both levels of organization we measured four stability properties: resistance, recovery, persistence, and invariability (Glossary, Fig. 2a-c, Table S2). We applied three disturbance types at four intensities. We distinguished disturbances that i) affect individuals selectively depending on their species identity, ii) affect individuals selectively depending on their location, and iii) affect all individuals similarly, irrespective of species identity or location (Fig. 2d,e,f). We tested the following hypotheses:

H1: At each level of organization, DS depends on disturbance type and intensity.

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

H2: All investigated stability properties exhibit positive pairwise correlations (Table S1).

H3: At each level of organization, the pair-wise correlations depend on disturbance type and intensity.

METHODS

Study systems

We used models representing the dynamics of the following communities: temperate forests (Bohn *et al.* 2014), a marine algal community (Baert *et al.* 2016a), a species-rich temperate grassland (May *et al.* 2009), a boreal predator-prey system of mustelids and voles (Radchuk *et al.* 2016a), and a temperate host-pathogen system of classical swine fever (CSF) virus affecting wild boar populations (Kramer-Schadt *et al.* 2009; Lange *et al.* 2012). All of these models had previously been parameterized to mimic the conditions of the respective natural communities (Table S3). All models have three aspects in common: 1) they are spatially explicit, describing the location of habitat patches and movement of individuals among them; 2) they include demographic stochasticity; and 3) the smallest modelled entity is the individual (except for the model simulating an algae community, which is based on Lotka-Volterra equations with a dispersal component; Supplementary Text T1). In addition to demographic stochasticity, two models (a host-pathogen model and a model of temperate forests) also include environmental stochasticity. Temperate grassland was modelled in two ways: using the original IBC-grass model (May *et al.* 2009) and a modified version that incorporates intra-specific trait variation (from now on referred to as Grassland ITV, Crawford *et al.* 2018). We thus used six models that represented five study systems. An advantage of using models that have been previously developed is ~~because~~ that those models have already been tested and verified for ~~respective~~ natural systems. We provide short summaries of the main processes included in each model in the Supplementary Methods, and more detailed descriptions of the models in the Supplementary Texts T1-T5.

Mis en forme : Anglais (États-Unis)

Disturbances

The previously published versions of the models, parameterized to reflect a stochastic quasi-equilibrium state (Nolting & Abbott 2016), were used as a control (no disturbance). We implemented disturbance as a one-time (pulse) removal of individuals. We implemented three types of disturbance (Fig. 2d, e, f): *random disturbance* affected individuals randomly, irrespective of their species identity and location. This disturbance type reflects a non-selective disturbance (De Laender *et al.* 2016). The *rare species removal disturbance* reflects the assumption that the rarest species are most extinction-prone (Solan *et al.* 2004) and is applied to species inversely to their population abundance ranks. This disturbance type was not possible in the wild boar - virus model (Supplementary Methods). The *spatially-structured disturbance* mimicked a localized disturbance by randomly selecting a point for the centre of the disturbance and then gradually increasing the disturbance radius around this point until the disturbance affected the target number of individuals (as defined by the disturbance intensity). We have implemented disturbance types via removal of individuals because this is a generic process that is inherent to several real-world disturbances, such as habitat fragmentation, hunting, culling and pollution. Using removal of individuals allows for comparability of results among the models as they differ in their processes. Therefore, removal of individuals was the best compromise among the relevance of the disturbance type and comparability of results among the systems.

Each disturbance type was implemented at four intensities, reflecting increasing proportions of the community that were removed (0.1, 0.2, 0.3 and 0.4 respectively). An upper bound of intensity was chosen via preliminary tests scanning a larger range of intensities, which

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

showed that at a disturbance intensity > 0.5, all species in our 2-species systems went extinct, complicating the measurements of all stability properties.

We ensured the comparability of the results in terms of the temporal scales among our study systems by scaling the duration of the simulation runs to the average generation length of all the species in the community (Pimm 1984). We used 30 average generations of the control as a 'burn-in' phase, after which either the control or one of the disturbance type scenarios were run for the next 60 generations, which was enough for majority of the species to attain either previous or a new stochastic quasi-equilibrium state (based on Gelman-Rubin diagnostics, Supplementary Figs. S1-S3, Supplementary Methods). The disturbance was applied in the first time step immediately after the 'burn-in' phase. We ran 30 replicates of each of the 13 scenarios (the control plus three disturbance types crossed with four levels of disturbance intensity) to account for the stochasticity inherent in the models. These 30 replicates were sufficient to capture effects that are due to disturbances and not merely a result of stochasticity (Supplementary Methods and Figs. S4-S7). The 'burn-in' phase was discarded when calculating the stability properties.

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Stability properties

At both the community and population level, we quantified four stability properties: *resistance*, *recovery*, *persistence* and *invariability* (Glossary, Fig. 2a-c, Table S2). We quantified stability properties analogously at both levels of organization. At the community level as state variable we used community composition, and at the population level we used abundance. We here detail how stability properties were measured at the community level, for details on how it was done at the population level please refer to Supplementary Methods.

Resistance was measured as Bray-Curtis similarity of the community composition between treatment and control at the first sampling after treatment (time step 1, Hillebrand *et al.* 2018). Resistance ranges between 0 and 1 with 1 reflecting maximum resistance (100% similarity between treatment and control). *Recovery* reflects the degree of restoration of the system at the end of the time series and was measured as Bray-Curtis similarity of the community composition between treatment and control at the final sampling (time step 60, Hillebrand *et al.* 2018). Analogously to resistance, recovery ranges between 0 and 1, with 1 reflecting a full recovery. *Persistence* was measured as the time during which the community composition in a treatment remains within 90% of the Bray-Curtis similarity with the composition of the control community. We scaled the original persistence values (min = 1, max = 60) by dividing them by their theoretically possible maximum (60), so that persistence ranges from 0 (the similarity between the treatment and control is < 0.9 in the first time step) to 1 (maximum persistence, a system remains within 90% of similarity during the whole period). Temporal *invariability* (Wang *et al.* 2017) was measured as the inverse of standard deviation of residuals from the linear model regressing the Bray-Curtis similarity between the treatment and control communities on time (Hillebrand *et al.* 2018). When temporal invariability is higher, i.e. when community composition fluctuates less around the average trend, the stability is higher. In Supplementary Methods we explain the choice of 1) Bray-Curtis similarity as a particularly suitable state variable for measuring stability at the community level (Donohue *et al.* 2013; Hillebrand *et al.* 2018) and 2) the threshold of 90% of Bray-Curtis similarity to measure persistence.

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

Dimensionality of stability

We quantified DS using multidimensional ellipsoids based on the covariance matrices among all stability properties (Donohue *et al.* 2013). The covariance matrices were constructed using the 30 replicates per scenario (at the community level) and per species nested within each scenario (at the population level). Since disturbances may affect both the volume and the shape of such ellipsoids (Donohue *et al.* 2013, Fig. 1a-c), we considered both. We used semi-axis lengths to characterize the shape of ellipsoids. The semi-axis length a_i was measured as $a_i = \lambda_i^{0.5}$, where λ_i is the i^{th} eigenvalue of the covariance matrix for a given scenario (i.e. a combination of the disturbance type and intensity) at the community level and for each species within each scenario at the population level. Ellipsoid volume was calculated as $V = \frac{\pi^{n/2}}{\Gamma(\frac{n}{2}+1)} \prod_{i=1}^{n} (\lambda^{0.5})$, where n is the dimensionality of the covariance matrix. Prior to the calculation of the ellipsoid volume, each set of semi-axis lengths was standardized by dividing all of them by the maximum length within a set, so that the maximum standardized length equalled 1. This allowed us to calculate the largest volume that was theoretically possible (i.e. all of the standardized semi-axis lengths are 1), which reflects a perfect spheroidal shape and, therefore, high DS. By dividing the actual ellipsoid volume by the theoretical maximum, we obtained a proportional volume. This proportional volume varies between 0 (a 'cigar'-like shape of ellipsoids, Fig. 1a), and 1 (a perfect sphere, Fig. 1b), reflecting low and high DS, respectively. Characterization of multidimensional ellipsoids based on covariance matrices relies on the assumption of linear relationships among stability properties (Supplementary Methods). In our case this assumption is satisfied for most study systems and disturbance types (e.g. Figs. S8-S15).

Mis en forme : Anglais (États-Unis)

To test the effect of disturbance properties on DS (H1) we fitted generalized mixed-effects models (Gamma distribution) with either ellipsoid volume or semi-axis length (per each rank, Fig. 1c) as a response (Supplementary Methods). As fixed effect predictors we included disturbance type (as a factor) and intensity (as a continuous variable). At the community level, we included study system as a random slope and at the population level, the random slope structure consisted of the species nested within the study system. We tested for the significance of fixed-effect terms using likelihood-ratio tests (LRT), but in our interpretations focused on effect sizes, because our study is based on simulations and virtually anything can become significant given enough replicates. At the community level, there was no variation in persistence for at least one disturbance type in the three study systems (persistence was 0 in all replicates of a rare species removal disturbance in both grassland systems and it was 1 in all replicates of random disturbance and rare species removal of the algae system). This precluded calculation of semi-axis lengths and ellipsoid volumes using all four stability properties (i.e. four dimensions) for these study systems. Therefore, we first fitted models using all four dimensions with only three study systems (forest, vole-mustelid, and wild boar-virus), and then used three dimensions (excluding persistence) to fit models with all six study systems. The results from both analyses are qualitatively the same. The results based on three dimensions are presented in the main text, and those based on four dimensions in Fig. S16, Tables S4 and S5.

Pair-wise correlations

To test whether all pair-wise correlations among stability properties were positive (H2) and affected by the disturbance properties (H3), we calculated Spearman-rank correlation for each pair of stability properties obtained for each of the 13 scenarios at the community level. Similarly, at the population level, Spearman-rank correlation was calculated for each species

within each scenario. Next, we transformed these Spearman-rank correlations into Fisher's z scores to improve their normality and to avoid any disproportionate influence of extreme values, and used them as effect sizes in the meta-analysis (Koricheva *et al.* 2013). We fitted mixed-effects meta-analytic models (Gaussian distribution) with the fixed effects of disturbance type (a factor), disturbance intensity (a continuous variable), and an interaction between them. At the community level, the models included the study system and replicate as random intercepts. At the population level, also species identity was included as a random intercept. All meta-analytic mixed-effects models were fitted with the library *metafor* in R (Viechtbauer 2010). All analyses were conducted in R 3.4.2 (R 2017).

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

RESULTS

Effect of disturbance properties on the dimensionality of stability

At the community level, neither disturbance type nor intensity affected DS (as measured by semi-axis lengths, Fig. 3a & Fig. S17a; and ellipsoid volumes, Fig. 4a & Fig. S18a; Table S4). However, study systems varied in their DS, as measured by semi-axis lengths (Table S6, Fig. 3a) or ellipsoid volumes (Fig. 4a). While grassland and forest communities were characterized by high DS (Fig. 4a), corresponding to spheroid-looking stability ellipsoids (Fig. S19a,b), vole-mustelid and algae communities had low DS, corresponding to a 'cigar'-like ellipsoids.

At the population level, the disturbance intensity did not affect DS (Fig. S18b), while disturbance type did (Table S4). Random disturbance increased DS (Fig. 4b). This was also reflected in the differences among semi-axis lengths: under random disturbance, the semi-axis lengths of the 1st rank were shorter ~~compared to~~than for other disturbance types, and the semi-axis lengths of the 3rd and 4th order were longer than for ~~compared to~~ other disturbance types (Fig. 3b). At the population level, DS varied among study systems and species (Fig. 4b, Table S5).

Pair-wise correlations between stability properties

At the community level, pair-wise correlations were on average positive (supporting H2) and three out of six correlations were affected by disturbance properties (supporting H3, Fig. 5a). The ~~Correlation~~ correlation of recovery with resistance and of recovery with invariability depended on the disturbance type, with positive correlations under random disturbance and very weak correlations (around 0) under spatially-structured disturbance. The ~~Correlation~~ correlations

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

between invariability and persistence became weaker and approached 0 as disturbance intensity increased.

At the population level, two pair-wise correlations were on average negative, three were positive, and one correlation was close to 0 (Fig. 5b-d). All pair-wise correlations were affected to a certain degree by disturbance type (Table S7). Additionally, disturbance intensity interacted with disturbance type in its effect on one correlation (invariability with recovery, Fig. 5c) and affected another one (invariability with resistance) in an additive way (Fig. 5d). There was no coherent pattern in how disturbance type modulated different pair-wise correlations.

DISCUSSION

We tested whether the correlation structure among stability properties was affected by ~~the~~ disturbance properties across five communities, differing in species richness and number of trophic levels. Contrary to our expectation (H1), ~~At the community level,~~ we did not find an effect of ~~the~~ disturbance properties on the dimensionality of stability~~–~~ (DS) at the community level~~(DS, H1)~~. At the population level, DS was higher under random disturbances. Additionally, at both levels of organization DS varied largely among study systems. At the community level, as expected (H2), we found generally positive correlations among different stability properties. In contrast, at the population level, the sign and magnitude of correlations were highly heterogeneous. Finally, pair-wise correlations at both levels depended on the disturbance properties, mainly on disturbance type, supporting our hypothesis (H3), although the effect sizes were smaller at the community level.

Dimensionality of stability at the community and population level

We did not find any effect of disturbance properties on DS at the community level. However, our findings reveal high heterogeneity in DS among study systems. For 4 of the 6 study systems, community stability was a highly-dimensional concept (Fig. 4a), suggesting that monitoring these systems requires measuring multiple stability properties. A promising avenue for future research would be investigating whether – and what – properties of a system predict its DS. At the community level, our findings indicate that such candidates of system properties as species richness and number of trophic levels do not discriminate the systems with low and high DS (Fig. S20a,b). Indeed, our two species-poor systems (‘vole-mustelid’ and ‘wild boar-virus’) exhibited strikingly different DS (Fig. 4a). Similarly, we observed both high and low DS in communities with either one (e.g. ‘algae’ vs ‘grassland’) or two trophic levels (‘vole-mustelid’

vs ‘wild boar-virus’). Taken together our results indicate that, although DS does not depend on disturbance properties, measuring multiple stability properties is necessary until we can establish whether and what system properties underlie DS.

Similarly to the community level, DS was highly context-dependent at the population level: in addition to variation among disturbance types, we also found high heterogeneity among study systems and species (Table S5), with the highest dimensionality under random disturbance. Although this type of disturbance may seem of little relevance to real-world applications, it is closely mimicked by the application of certain chemicals (Roessink *et al.* 2006; DeLaender *et al.* 2016), and therefore its effects on DS deserve further investigations. Interestingly, our findings indicate that species-poor systems may generally have higher DS (Fig. S20d). Since population invariability is known to be lower in species-rich systems (Gonzalez & Descamps-Julien 2004; Jiang & Pu 2009; Gross *et al.* 2014), it is likely that species richness modulates the relations of population-level invariability with other stability properties. However, as we did not experimentally manipulate species richness in this study, this is a hypothesis to be tested by future research.

Reflecting the context-dependence of DS, all pair-wise correlations between population stability properties depended on the disturbance type, and additionally two out of six depended on the disturbance intensity (Fig. 5b-d). These results corroborate earlier analytical derivations (Harrison 1979) that showed that the relation between population resilience and resistance depends both on density-dependence and on the environmental sensitivity of the population growth rate. In fact, the high heterogeneity found in the meta-analytic models testing the context-dependence of the pair-wise correlations between population stability properties (Table S8) points towards species-specific differences which may be due to differences in density

Mis en forme : Anglais (États-Unis)
Code de champ modifié
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

dependence (as found by Harrison 1979) or any other species-specific properties (e.g. population growth, carrying capacity).

From a monitoring perspective, the context-dependence of the correlative structure among stability properties at the population level (H3) means that quantification of population stability as a whole requires measurements of multiple stability properties unless the context-dependence of these properties was established beforehand. Even though this may sound like a daunting task, it is already a well-established practice within population viability analysis (Beissinger & Westphal 1998; Pe'er *et al.* 2013). In such studies, multiple stability properties such as time to extinction, minimum viable population size, mean population size, etc. are jointly reported as a rule (Pe'er *et al.* 2013).

Across-system differences in dimensionality of stability and plausible mechanisms

We did not find any effect of disturbance type on DS at the community level but higher DS was observed for random disturbances at the population level. Although these general results hold across the five different study systems, the largest heterogeneity in DS was revealed among study systems. As mentioned above, this heterogeneity cannot be explained by system properties as species richness and number of trophic levels. Two general mechanisms behind the responses of ~~system's~~ DS to disturbance can be distinguished: changes in the intensity of species interactions and changes in the degree of stochastic dynamics of the system. Although we have not experimentally manipulated these mechanisms here, we discuss the revealed differences in DS among systems in light of these mechanisms.

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)

Changes in the intensity of species interactions could explain the link between disturbances and DS. Indeed, previous research demonstrated that inter- and intra-specific interactions affect community stability (McCann 2000; Thébault & Loreau 2005; Barabás *et al.* 2016). Moreover, the effect of changes in species interactions on DS may differ depending on the primary type of interactions within a system (competitive vs. trophic), because vertical diversity was shown to modulate the biodiversity – stability relationship (Reiss *et al.* 2009; Radchuk *et al.* 2016b)+Wang and Brose's Ecology Letters from last year ('vertical diversity hypothesis'). Indeed, in our simulations, the removal of a rare species ~~removal in~~ from communities driven by competitive interactions (algae, grassland and forest systems) resulted in lower DS (Table S9) both at the community and population level. The mechanism underlying the lower DS in these communities after removal of rare species (Table S9) may be an increasing strength of competitive interactions among the remaining species.

Stronger competitive interactions presumably occurring after removal of rare species, may in turn lead to more deterministic dynamics of the system. The degree of dynamic system behaviour may itself affect DS. Indeed, ~~a~~ more stochastic population dynamics likely result~~s~~ in weaker pair-wise correlation among stability properties, thus leading to higher DS. In support of this expectation, we found increased DS after a spatially-structured disturbance in systems consisting of two strongly interacting species at different trophic levels (Table S9). Such two-species communities are presumably more prone to stochastic effects than multispecies communities, and therefore exhibit the above-described behaviour. To closer inspect the relation between system stochastic behaviour and DS, we used population abundance and community evenness ~~the following~~as proxies of the influence of demographic stochasticity ~~at the~~ on populations and ~~community~~ communities~~level~~, respectively~~:~~ ~~population abundance and~~

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Code de champ modifié

~~community evenness~~ (Supplementary Methods). Overall, we found an increase in DS under higher stochasticity at both population and community levels (Fig. S21-S22). However, the responses varied among disturbance types, study systems and species (for the population-level DS; Figs S23-S24). ~~Importantly, these findings have to be treated with caution because~~ Clearly, we did not experimentally vary stochasticity, as this was not the goal of our study~~.~~, and ~~Future~~ future research in this direction is warranted.

The change of system behaviour from stochastic to deterministic and vice versa may also be caused by dispersal. Dispersal plays an important role in stochastic community assembly (Chase 2007) and has recently attracted attention in the context of metapopulation and metacommunity stability (Dai *et al.* 2013; De Raedt *et al.* 2017; Gilarranz *et al.* 2017; Zelnik *et al.* 2018). Further, functional diversity, in particular response diversity and correlations among effect and response traits were suggested as mechanisms potentially explaining pair-wise correlations between stability properties (Pennekamp *et al.* 2018). Additionally, some of the observed differences in system responses may be due to the model type used and not especially because of the system-specific characteristics. Thus, models such as the Lotka-Volterra model (used for the algae community) result in more deterministic community dynamics compared to individual-based models that incorporate more stochasticity at different levels and processes. Indeed, the algae model showed a strikingly clear response as compared to other systems (Table S9, Fig. 4a), which may be explained by deterministic system behavior.

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Commenté [FDL2]: Not clear what we mean here.

Challenges and future research

Our study identified several challenges associated with measuring DS~~,~~. ~~for example~~ Amongst those are: quantifying the relationships among stability properties that are non-linearly related;~~,~~ choosing appropriate state variables to measure stability properties;~~,~~ choosing specific stability

properties at each level of organization~~;~~, deciding on the disturbance types and intensity levels. A wide variety of stability properties is used in the literature, and different approaches to quantifying them are available (Grimm & Wissel 1997; Ingrisch & Bahn 2018). For example, we have chosen to measure resistance at the first time step after disturbance. An alternative would be to measure resistance at the time step when the response is the strongest, which, naturally, will differ among species and systems. Comparison of how existing stability properties and methods to measure them perform under different conditions and unification of such approaches ~~must be~~is an avenue for future research (Ingrisch & Bahn 2018). Further, we here focused on disturbance by removing individuals mainly for the sake of comparability of results among systems and models. What the implications of other disturbance types are, in particular the addition of individuals (stocking) and habitat fragmentation ~~are~~, and how they compare to the removal of individuals, remains to be tested.

Further, a future research agenda on DS should include: a mechanistic (?) investigation of interactions among disturbance types, developing approaches to quantify non-linear responses of systems to disturbance, and non-linear trade-offs among dimensions of stability. Importantly, understanding the ~~mechanistic~~ mechanisms underpinning~~s~~ ~~of~~ the responses of DS requires that future experiments on real and *in-silico* systems manipulate potential mechanisms, generally the strength and sign of species interactions, and the stochasticity of the system's dynamics (which may be achieved by manipulating response diversity, dispersal abilities and environmental sensitivities of the species in the community). [What I cut may be a bit too evident] ~~Preferably, such experiments would use a factorial design combining several tentative mechanisms of DS, while measuring population or community dynamics at a fine temporal resolution.~~ For such experiments the use of modelling studies, as done here, seems ~~indispensable~~a useful ay forward,

Code de champ modifié

Code de champ modifié

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

because collection of such data empirically is feasible only in micro- and mesocosm settings (Baert *et al.* 2016b; Garnier *et al.* 2017; Karakoç *et al.* 2018; Pennekamp *et al.* 2018). Importantly, although measuring DS was rather easy in our modelling study, empirical studies may be limited because of the difficulty to measure multiple stability properties in natural systems.

There is a large, continually growing literature on stochastic population, community and metacommunity ecology, which considers relationships between (usually only two) different stability properties at different levels of organisation, and includes age-, stage- and spatial structure (e.g. Petchey *et al.* 1997; Ovaskainen & Hanski 2002; Inchausti & Halley 2003; de Mazancourt *et al.* 2013; Arnoldi *et al.* 2016; Wang & Loreau 2016). We here point out avenues for extending the current research and underline that both empirical and theoretical efforts are needed.

Conclusions

We used process-based models developed and parameterized to reflect a range of natural systems to test the effect of disturbance properties on the dimensionality of stability measured at the population and community level. Our findings indicate that in the majority of cases monitoring of population and community stability will require quantification of multiple stability properties, and the use of a single proxy is not justified (Donohue *et al.* 2013; Hillebrand *et al.* 2018). Moreover, we also show that the correlations among stability properties may differ depending on the level of organization, which was demonstrated only once until now by Hillebrand et al. (2018)~~, who considered~~ who compared the community ~~and~~ and ecosystem level~~s~~. We believe that our study will catalyze the emerging research on the relations among stability properties measured at different organization levels, and temporal and spatial scales,

Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Mis en forme : Anglais (États-Unis)
Code de champ modifié
Code de champ modifié

which in turn will lead to the development of a comprehensive theory of community and population dynamics further from their equilibrium.

ACKNOWLEDGEMENTS

This manuscript was initiated at the session 'Ecological models as tools to assess persistence of ecological systems in face of environmental pressures' organized by VR and SKS at the EcoSummit 2016 conference. We are grateful to Alban Sagouis and four anonymous reviewers for their feedback on the manuscript draft. CS was supported by the BioMove Research Training Group of the German Research Foundation (DFG-GRK 2118/1), MC was funded by DFG Priority Program 1374, "Infrastructure-Biodiversity-Exploratories" (DFG-JE 207/5-1) and JDR by the Research Foundation Flanders (Grant no FWO14/ASP/075). FDL received support from the Fund for Scientific Research, FNRS (PDR T.0048.16). JCS considers this work a contribution to his VILLUM Investigator project "Biodiversity Dynamics in a Changing World" funded by VILLUM FONDEN (grant 16549).

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

Mis en forme : Anglais (États-Unis)

LITERATURE CITED

Arnoldi, J.F., Loreau, M. & Haegeman, B. (2016). Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. *J. Theor. Biol.*, 389, 47–59

Baert, J.M., Janssen, C.R., Sabbe, K. & De Laender, F. (2016a). Per capita interactions and stress tolerance drive stress-induced changes in biodiversity effects on ecosystem functions. *Nat. Commun.*, 7, 12486

Baert, J.M., De Laender, F., Sabbe, K. & Janssen, C.R. (2016b). Biodiversity increases functional and compositional resistance, but decreases resilience in phytoplankton communities. *Ecology*, 97, 3433–3440

Barabás, G., J. Michalska-Smith, M. & Allesina, S. (2016). The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *Am. Nat.*, 188, E1–E12

Beissinger, S.R. & Westphal, M.I. (1998). On the use of demographic models of population viability in endangered species management. *J. Wildl. Manage.*, 62, 821–841

Bohn, F.J., Frank, K. & Huth, A. (2014). Of climate and its resulting tree growth: Simulating the productivity of temperate forests. *Ecol. Modell.*, 278, 9–17

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W. a, Cline, T., *et al.* (2011). Early warnings of regime shifts: a whole-ecosystem experiment. *Science*, 332, 1079–1082

Chase, J.M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. U. S. A.*, 104, 17430–17434

Crawford, M., Jeltsch, F., May, F., Grimm, V. & Schlaegel, U. (2018). Intraspecific trait variation increases species diversity in a trait-based grassland model. *Oikos*, 00, 1–15

Mis en forme : Anglais (États-Unis)

532 Dai, L., Korolev, K.S. & Gore, J. (2013). Slower recovery in space before collapse of
533 connected populations. *Nature*, 496, 355–358

534 Dai, L., Korolev, K.S. & Gore, J. (2015). Relation between stability and resilience
535 determines the performance of early warning signals under different environmental drivers.
536 *Proc. Natl. Acad. Sci.*, 112, 10056–10061

537 Dakos, V., Van Nes, E.H., D'Odorico, P. & Scheffer, M. (2012). Robustness of variance
538 and autocorrelation as indicators of critical slowing down. *Ecology*, 93, 264–271

539 DeLaender, F., Rohr, J.R., Aschahuer, R., Baird, D., Berger, U., Eisenhauer, N., *et al.*
540 (2016). Re-introducing environmental change drivers in biodiversity-ecosystem functioning
541 research. *Trends Ecol. Evol.*, 31, 905–915

542 Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., *et*
543 *al.* (2016). Navigating the complexity of ecological stability. *Ecol. Lett.*, 19, 1172–1185

544 Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., Mcnally, L., Viana, M., *et al.*
545 (2013). On the dimensionality of ecological stability. *Ecol. Lett.*, 16, 421–429

546 Garnier, A., Pennekamp, F., Lemoine, M. & Petchey, O.L. (2017). Temporal scale
547 dependent interactions between multiple environmental disturbances in microcosm ecosystems.
548 *Glob. Chang. Biol.*, 23, 5237–5248

549 Gilarranz, L.J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J. & Gonzalez, A. (2017).
550 Effects of network modularity on the spread of perturbation impact in experimental
551 metapopulations. *Science*, 357, 199–201

552 Ginzburg, L.R., Slobodkin, L.B., Johnson, K. & Bindman, A.G. (1982). Quasiextinction
553 probabilities as a measure of impact on population growth. *Risk Anal.*, 2, 171–181

554 Gonzalez, A. & Descamps-Julien, B. (2004). Population and community variability in
555 randomly fluctuating environments. *Oikos*, 106, 105–116

556 Grimm, V. & Wissel, C. (1997). Babel, or the ecological stability discussions: An
557 inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109, 323–
558 334

559 Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Polley, H.W., *et al.*
560 (2014). Species Richness and the Temporal Stability of Biomass Production: A New Analysis of
561 Recent Biodiversity Experiments. *Am. Nat.*, 183, 1–12

562 Harrison, G.W. (1979). Stability under environmental stress: Resistance, resilience,
563 persistence, and variability. *Am. Nat.*, 113, 659–669

564 Higgins, S.I. & Scheiter, S. (2012). Atmospheric CO2 forces abrupt vegetation shifts
565 locally, but not globally. *Nature*, 488, 209–212

566 Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö. & Striebel, M.
567 (2018). Decomposing multiple dimensions of stability in global change experiments. *Ecol. Lett.*,
568 21, 21–30

569 Inchausti, P. & Halley, J. (2003). On the relation between temporal variability and
570 persistence time in animal populations. *J. Anim. Ecol.*, 72, 899–908

571 Ingrisch, J. & Bahn, M. (2018). Towards a Comparable Quantification of Resilience.
572 *Trends Ecol. Evol.*, 33, 251–259

573 Jiang, L. & Pu, Z. (2009). Different Effects of Species Diversity on Temporal Stability in
574 Single-Trophic and Multitrophic Communities. *Am. Nat.*, 174, 651–659

575 Karakoç, C., Radchuk, V., Harms, H. & Chatzinotas, A. (2018). Interactions between

predation and disturbances shape prey communities. *Sci. Rep.*, 8, 2968

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press

Kramer-Schadt, S., Fernandez, N., Eisinger, D., Grimm, V. & Thulke, H.H. (2009). Individual variations in infectiousness explain long-term disease persistence in wildlife populations. *Oikos*, 118, 199–208

De Laender, F., Rohr, J.R., Ashauer, R., Baird, D.J., Berger, U., Eisenhauer, N., *et al.* (2016). Reintroducing Environmental Change Drivers in Biodiversity–Ecosystem Functioning Research. *Trends Ecol. Evol.*, 31, 905–915

Lange, M., Kramer-Schadt, S., Blome, S., Beer, M. & Thulke, H.-H. (2012). Disease severity declines over time after a wild boar population has been affected by classical swine fever - legend or actual epidemiological process? *Prev. Vet. Med.*, 106, 185–195

May, F., Grimm, V. & Jeltsch, F. (2009). Reversed effects of grazing on plant diversity: The role of below-ground competition and size symmetry. *Oikos*, 118, 1830–1843

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B., *et al.* (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.*, 16, 617–625

McCann, K.S. (2000). The diversity-stability. *Nature*, 405, 228–233

Nolting, B.C. & Abbott, K.C. (2016). Balls, cups, and quasi-potentials: Quantifying stability in stochastic systems. *Ecology*, 97, 850–864

Ovaskainen, O. & Hanski, I. (2002). Transient Dynamics in Metapopulation Response to Perturbation. *Theor. Popul. Biol.*, 61, 285–295

598 Pe'er, G., Matsinos, Y.G., Johst, K., Franz, K.W., Turlure, C., Radchuk, V., *et al.* (2013).
599 A protocol for better design, application, and communication of population viability analyses.
600 *Conserv. Biol.*, 27, 644–656

601 Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, I., *et al.* (2018).
602 Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109–112

603 Petchey, O.L., Gonzalez, A. & Wilson, H.B. (1997). Effects on population persistence:
604 the interaction between environmental noise colour, intraspecific competition and space. *Proc. R.*
605 *Soc. B-Biological Sci.*, 264, 1841–1847

606 Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326

607 R. (2017). R Core Team. R: A language and environment for statistical computing.

608 Radchuk, V., Ims, R.A. & Andreassen, H.P. (2016a). From individuals to population
609 cycles: The role of extrinsic and intrinsic factors in rodent populations. *Ecology*, 97, 720–732

610 Radchuk, V., De Laender, F., Van den Brink, P.J. & Grimm, V. (2016b). Biodiversity
611 and ecosystem functioning decoupled: invariant ecosystem functioning despite non-random
612 reductions in consumer diversity. *Oikos*, 125, 424–433

613 De Raedt, J., Baert, J.M., Janssen, C.R. & De Laender, F. (2017). Non-additive effects of
614 dispersal and selective stress on structure, evenness, and biovolume production in marine diatom
615 communities. *Hydrobiologia*, 788, 385–396

616 Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009). Emerging horizons in
617 biodiversity and ecosystem functioning research. *Trends Ecol. Evol.*, 24, 505–514

618 Roessink, I., Crum, S.J.H., Bransen, F., Van Leeuwen, E., Van Kerkum, F., Koelmans,
619 A.A., *et al.* (2006). Impact of triphenyltin acetate in microcosms simulating floodplain lakes. I.

Influence of sediment quality. *Ecotoxicology*, 15, 267–293

Scheffer, M., Carpenter, S.R., Dakos, V. & van Nes, E.H. (2015). Generic Indicators of Ecological Resilience: Inferring the Chance of a Critical Transition. *Annu. Rev. Ecol. Evol. Syst.*, 46, 145–167

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. & Srivastava, D.S. (2004). Extinction and ecosystem function in the marine benthos. *Science*, 306, 1177–1180

Thébault, E. & Loreau, M. (2005). Trophic Interactions and the Relationship between Species Diversity and Ecosystem Stability. *Am. Nat.*, 166, E95–E114

Turner, M.G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, 91, 2833–2849

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Softw.*, 36, 1–48

Wang, S. & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.*, 19, 510–518

Wang, S., Loreau, M., Arnoldi, J.F., Fang, J., Rahman, K.A., Tao, S., *et al.* (2017). An invariability-area relationship sheds new light on the spatial scaling of ecological stability. *Nat. Commun.*, 8, 15211

Zelnik, Y.R., Arnoldi, J.F. & Loreau, M. (2018). The three regimes of spatial recovery. *bioRxiv*

FIGURES

Figure 1. Schematic representation of the dimensionality of stability. (a,b) Hypothetical multidimensional ellipsoids reflecting systems with low (a, black) and high (b, brown) dimensionality, and their respective semi-axis lengths (c), reflecting the amount of variation along each axis. The axes are ranked from the one that explains most variation to the one with the least variation (Donohue et al. 2013).

Figure 2. (a-c) Four stability properties measured at the community (a) and population (b, c) level in this study. Red vertical dotted line highlights the time step at which the disturbance (= treatment) occurs (for demonstration purpose here generation 4). Resistance (*Res*) and recovery (*Rec*) at the community level are measured as $BC\left(\frac{Comp_t}{Comp_c}\right)$, where *BC* is Bray-Curtis similarity, and $Comp_x$ is community composition in either control (x = c) or treatment (x = t), measured at the time steps indicated by green (*Res*) and blue (*Rec*) vertical dashed lines, respectively. Resistance and recovery at the population level are measured as $\ln(\frac{Ab_t}{Ab_c})$, where Ab_x is abundance in either control (x = c) or treatment (x = t), measured at the time steps indicated by green (*Res*) and blue (*Rec*) vertical dashed lines, respectively. The grey solid line depicts a fitted model that is used to assess invariability (*Inv*), for demonstration purpose only two residuals are highlighted. An orange arrow shows how (a) $T_{0.9}$ at the community level and (c) TTE (time to extinction) at the population level are obtained. Persistence at the population level is calculated as: $Perc_{pop} = \frac{TTE}{T_{max}}$; and at the community level: $Perc_{com} = \frac{T_{0.9}}{T_{max}}$, where T_{max} is the maximum duration (here 16 generations) (for more details see Methods and Table S2). (d-f). Disturbance types used in this study: random (d), rare species removal (e) and spatially-structured disturbance (f). Each disturbance type is shown at 20% disturbance intensity. A two-patch system is depicted with

Mis en forme : Anglais (États-Unis)

663 each symbol representing an individual and the shape reflecting the species identity. Empty
664 symbols indicate the individuals that would be removed under each disturbance. A circle in (f)
665 shows a radius of a spatially-structured disturbance type.

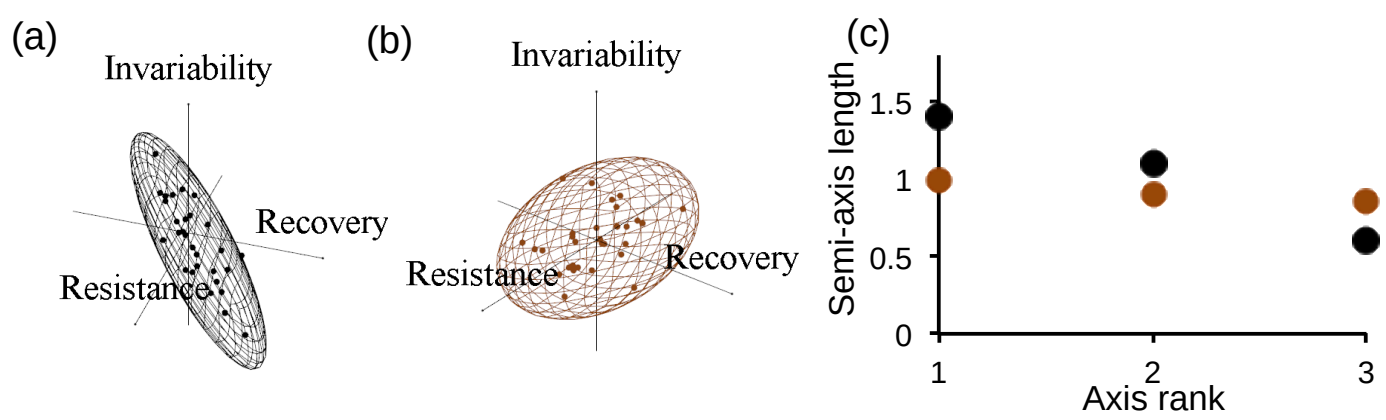
666 Figure 3. At the community level (a) disturbance type did not affect semi-axis lengths,
667 whereas at the population level (b) semi-axis lengths were affected by the disturbance type. High
668 DS was found under random disturbance, as indicated by the semi-axis lengths of the 1st rank on
669 average shorter compared to other disturbance types, and the semi-axis lengths of the 3rd and 4th
670 order longer compared to other disturbance types. We observed large variation among study
671 systems in their semi-axis lengths. Results are shown for disturbance intensity = 0.2 (since there
672 is no effect of intensity). The semi-axis lengths are shown for each rank separately (1-3 for the
673 community and 1-4 for the population level). The dots show outliers. Study systems are
674 described in Table S3, different colours reflect different disturbance types: spatially-structured,
675 rare species removal and random disturbance.

676 Figure 4. Disturbance type did not affect proportional ellipsoid volumes at the
677 community (a), but did affect them at the population (b) level: random disturbance increased the
678 dimensionality of stability, as visible from larger ellipsoid volume. We observed large variation
679 among study systems in their ellipsoid volumes, especially at the community level. Results are
680 shown for disturbance intensity = 0.2 (since there is no effect of intensity). At the maximum
681 proportional volume (= 1) DS is highest, corresponding to a perfect sphere. The lower the
682 proportional volume the lower is DS, with ellipsoid shape changing via a 'frisbee'-looking to a
683 'cigar'-like shape. Ellipsoids at the community and population level are calculated using three
684 and four dimensions, respectively (see Methods). Abbreviations are as in Fig. 3.

Mis en forme : Anglais (États-Unis)

685 Figure 5. Effects of disturbance type and intensity on Fisher's z scores representing all
686 pair-wise correlations between stability properties at the community (a) and population (b-d)
687 level. At the community level, majority of correlations were positive (a), whereas at the
688 population level, the sign and magnitude of correlations were highly heterogeneous (b-d).
689 Disturbance type affected two out of six correlations at the community level and all correlations
690 at the population levels. Shown are the effect sizes (and their 95 % CI) from the model that
691 described the data the best. For those correlations not affected by tested variables the effect size
692 obtained with the model including the intercept only is shown (i.e. the effect across all study
693 cases). Abbreviations are as in Fig. 3.
694

695 Figure 1.



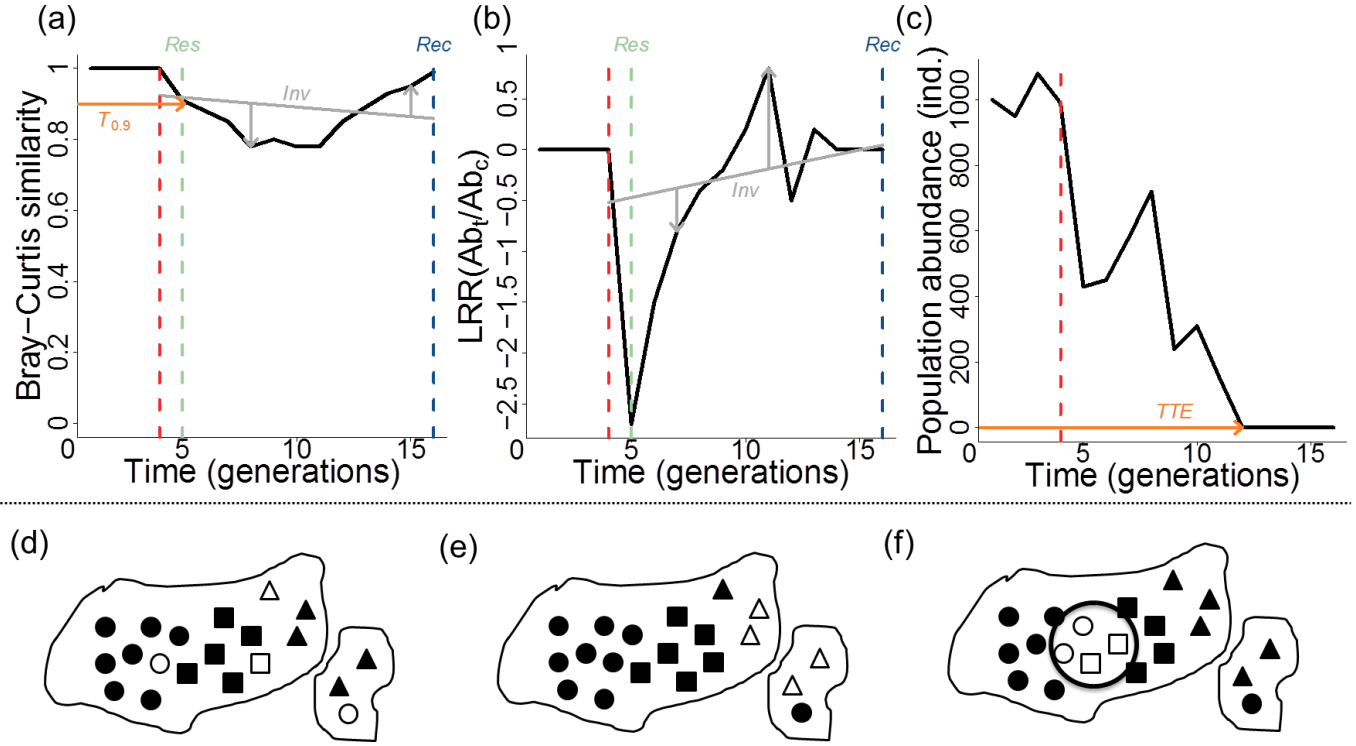
696

697

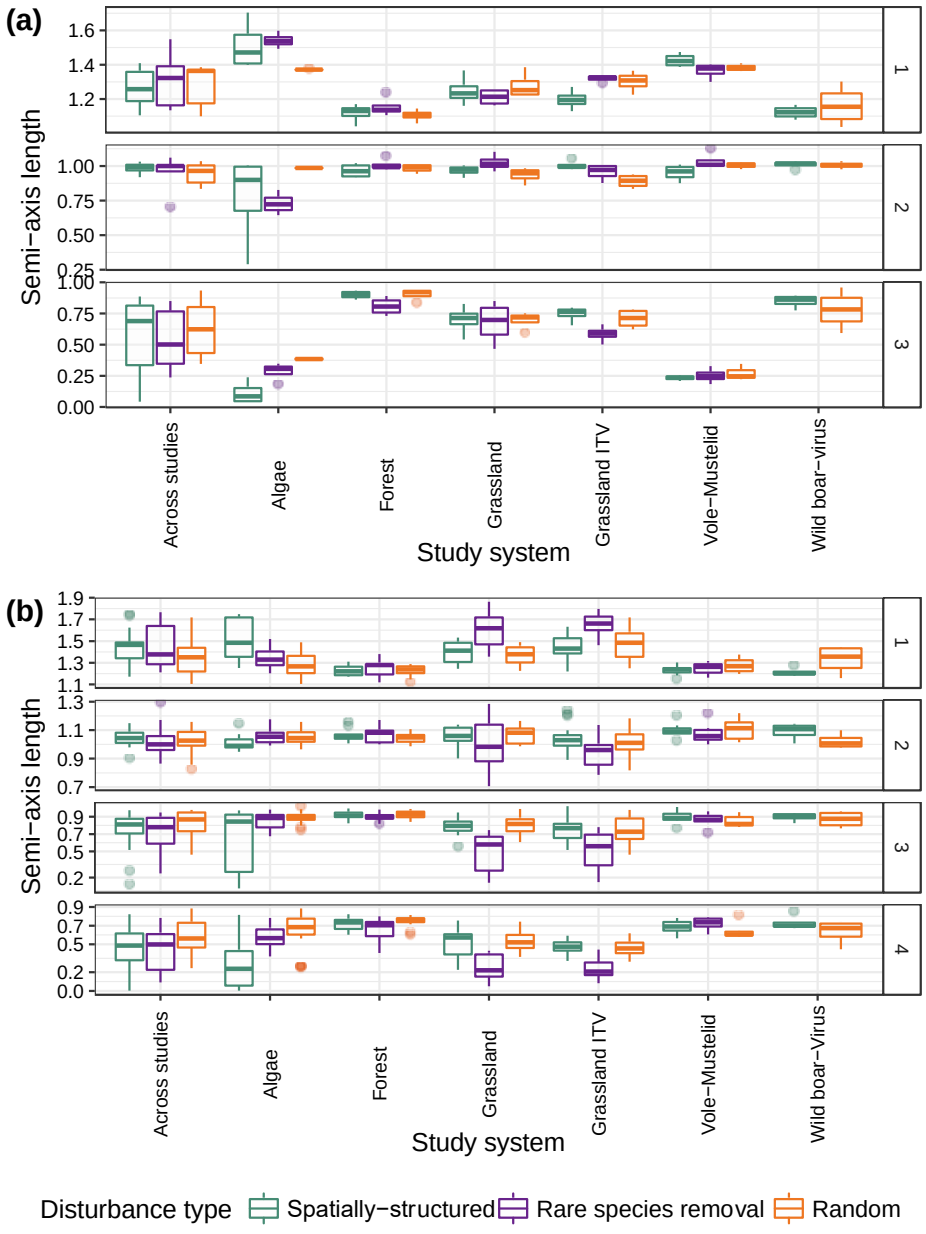
698

699

Figure 2.

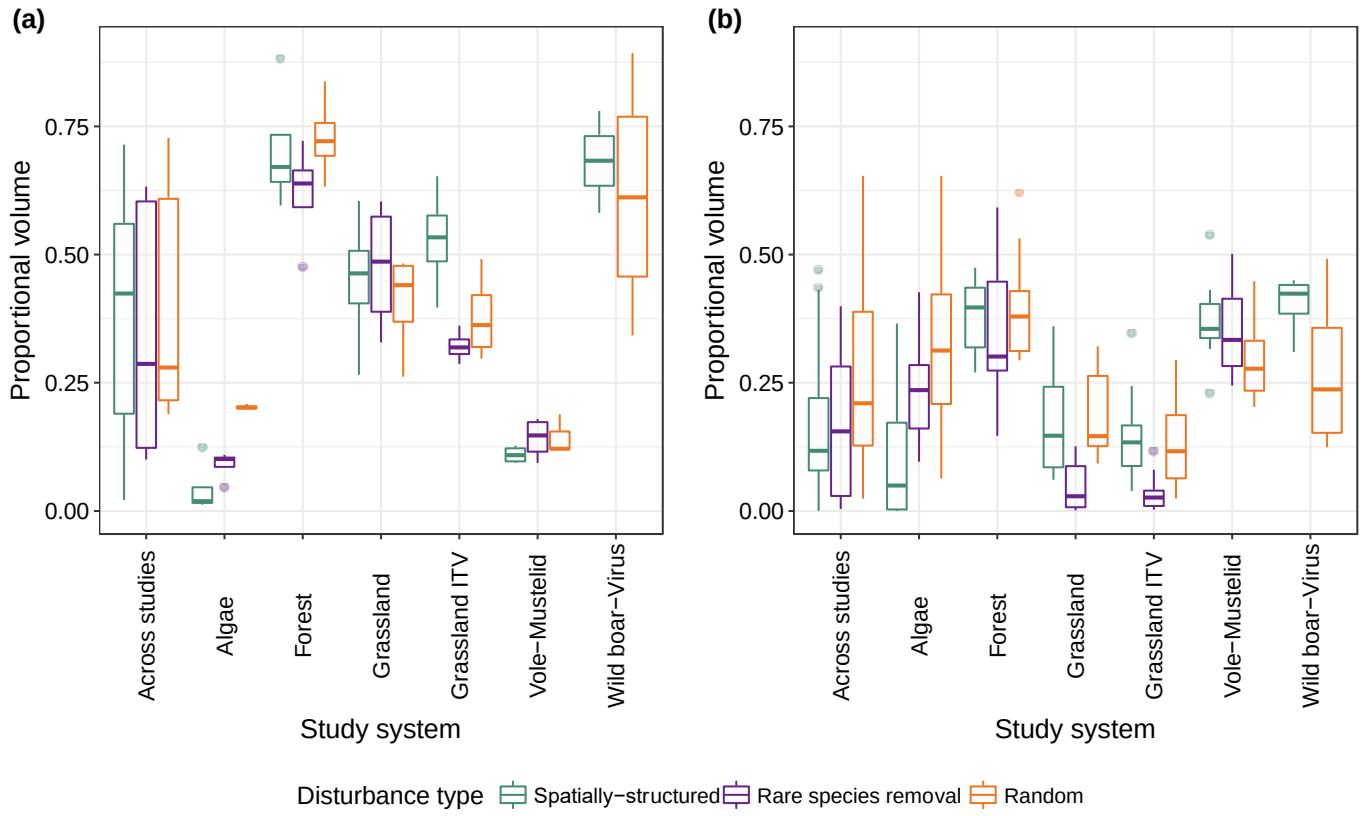

(a)
(b)
(c)
Res
Rec
Inv
$T_{0.9}$
Bray−Curtis similarity
LRR(Ab_t/Ab_c)
Population abundance (ind.)
TTE
Time (generations)
(d)
(e)
(f)

703 Figure 3.



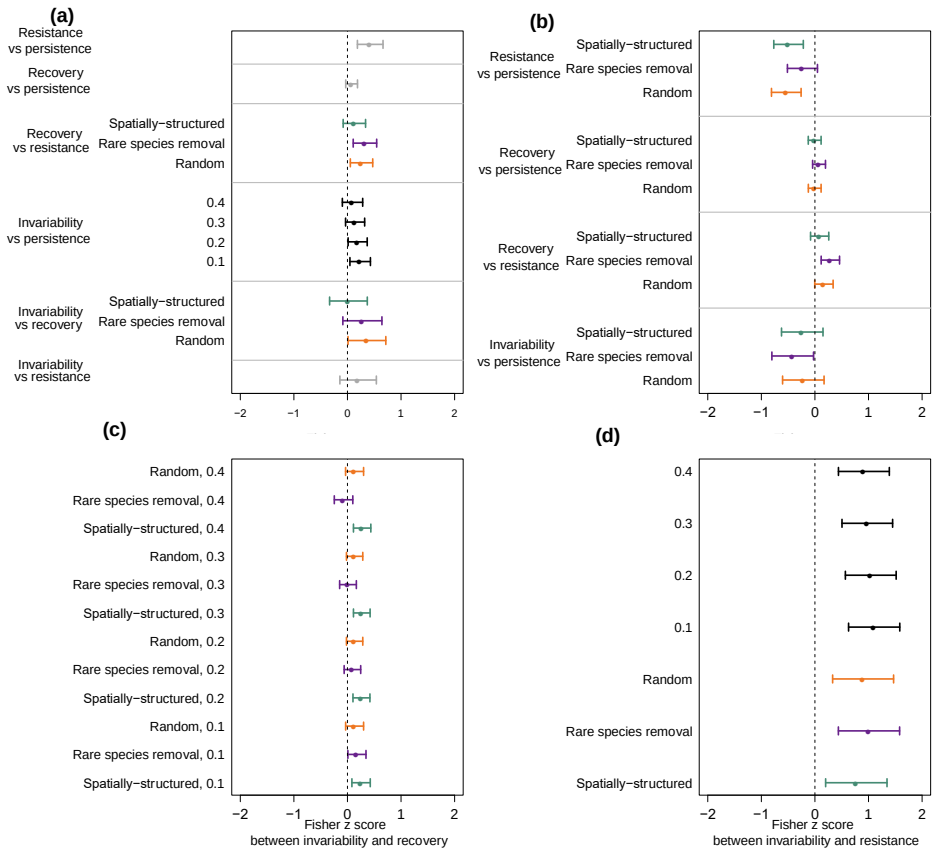
704

705 Figure 4.



706

Figure 5.


(a)
Resistance vs persistence
Recovery vs persistence
Recovery vs resistance
Spatially−structured
Rare species removal
Random
Invariability vs persistence
0.4
0.3
0.2
0.1
Invariability vs recovery
Spatially−structured
Rare species removal
Random
Invariability vs resistance
−2 −1 0 1 2
(b)
Resistance vs persistence
Recovery vs persistence
Recovery vs resistance
Invariability vs persistence
Spatially−structured
Rare species removal
Random
−2 −1 0 1 2
(c)
Random, 0.4
Rare species removal, 0.4
Spatially−structured, 0.4
Random, 0.3
Rare species removal, 0.3
Spatially−structured, 0.3
Random, 0.2
Rare species removal, 0.2
Spatially−structured, 0.2
Random, 0.1
Rare species removal, 0.1
Spatially−structured, 0.1
−2 −1 0 1 2
Fisher z score
between invariability and recovery
(d)
0.4
0.3
0.2
0.1
Random
Rare species removal
Spatially−structured
−2 −1 0 1 2
Fisher z score
between invariability and resistance